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A user's guide to functional diversity indices

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Abstract. Functional diversity is the diversity of species traits in ecosystems. This concept is increasingly used in ecological research, yet its formal definition and measurements are currently under discussion. As the overall behavior and consistency of functional diversity indices have not been described so far, the novice user risks choosing an inaccurate index or a set of redundant indices to represent functional diversity.

In our study we closely examine functional diversity indices to clarify their accuracy, consistency, and independence. Following current theory, we categorize them into functional richness, evenness, or divergence indices. We considered existing indices as well as new indices developed in this study. The new indices aimed at remedying the weaknesses of currently used indices (e.g., by taking into account intraspecific variability). Using virtual data sets, we test (1) whether indices respond to community changes as expected from their category and (2) whether the indices within each category are consistent and independent of indices from other categories. We also test the accuracy of methods proposed for the use of categorical traits.

Most classical functional richness indices either failed to describe functional richness or were correlated with functional divergence indices. We therefore recommend using the new functional richness indices that consider intraspecific variability and thus empty space in the functional niche space. In contrast, most functional evenness and divergence indices performed well with respect to all proposed tests. For categorical variables, we do not recommend blending discrete and real-valued traits (except for indices based on distance measures) since functional evenness and divergence have no transposable meaning for discrete traits. Nonetheless, species diversity indices can be applied to categorical traits (using trait levels instead of species) in order to describe functional richness and equitability.

Key words: categorical variables; functional divergence; functional evenness; functional richness; morphological traits; species richness.

Introduction

Biodiversity is commonly expressed through indices based on species richness and species abundances (Whittaker 1972, Lande 1996, Purvis and Hector 2000). Recently, however, studies focused on diversity have begun to incorporate the concept of functional diversity. In contrast to species diversity, functional diversity measures the distribution and the range of what organisms do in communities and ecosystems and thus considers the complementarity and redundancy of co-occurring species (Díaz and Cabido 2001, Petchey and Gaston 2006). Functional diversity is commonly assumed to be a better predictor of ecosystem productivity and vulnerability than species diversity (Tilman et al. 1997, Hulot et al. 2000, Díaz and Cabido 2001, Heemsbergen et al. 2004).

Including species' functions in the measurement of biodiversity is a relatively recent approach. Since 1990, the number of publications based on functional diversity has been steadily increasing (Fig. 1). Although the concept of functional diversity itself is relatively simple to understand, its increasing importance in biodiversity studies has revealed that measuring it is a complex endeavor: while studies focused on species diversity only need to count individuals from different species (i.e., sort them into several categories), functional diversity studies have to describe a multidimensional cloud of points in trait space (i.e., each coordinate corresponds to a measured trait), each point representing an individual or a species. Several methods have recently been proposed to help identify the necessary measures of functional diversity (reviewed in Ricotta 2005, Petchey and Gaston 2006, Podani and Schmera 2007, Villéger et al. 2008). Two main approaches have emerged: on the one hand, functional groups can be defined based on few behavioral/morphological characteristics (e.g., diet affinities, food acquisition methods, preferred habitat) and the observed species are assigned to different functional categories (Bremner et al. 2003, Stevens et al. 2003, Petchey and Gaston 2006). These data can be further processed with conventional species diversity indices (functional group richness, Shannon index, Simpson diversity index, etc.; e.g., Stevens et al. 2003). This approach is suitable for macro-ecological studies since

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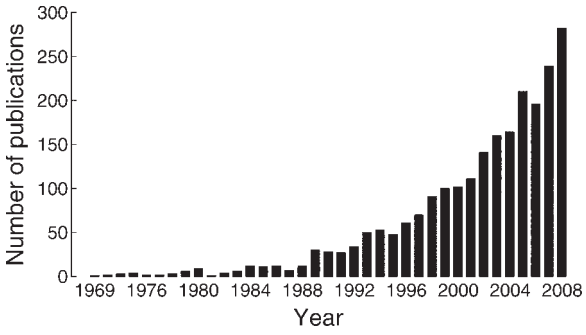

FIG. 1. Number of publications containing the term "functional diversity" in title, abstract, or key words. Source: Scopus ⟨http://www.scopus.com/scopus/search/form.url⟩ to 31 December 2008.

information on species assignment to functional groups is available for a broad range of species and generally easy to obtain. Furthermore, such studies only need a low level of detail in contrasting species traits. On the other hand, functional diversity can be calculated based on specific functional traits measured for each species. This approach promises a finer resolution (Bremner et al. 2003, Petchey and Gaston 2006), but trait values are more difficult to obtain than information on functional group memberships. For instance, it is easier to categorize fish species by their general diet than to obtain measurements on their size, gape width, stomach length, etc. Functional traits can be morphological traits that represent adaptations to different diets or habitats, physiological traits (e.g., temperature tolerance), reproductive traits (e.g., number of eggs and egg diameter), or behavioral traits (e.g., migratory behavior or parental care) (Bremner et al. 2003, Dumay et al. 2004, Lepš et al. 2006). Because most of these measurements are real-valued (i.e., not discrete) and more than one trait is used to describe the different functions, the indices commonly used to measure species diversity cannot be applied (e.g., Simpson diversity index).

To make use of multiple trait measurements, Bremner et al. (2003) compared functional trait compositions between sites using principal components (PCA) or co-inertia analyses. However, this approach is comparative and not based on functional diversity per se and therefore does not give absolute insight into the distribution of traits within a specific site. Alternatively, species diversity indices have now been transposed to functional diversity measurements, and several new indices have been proposed (e.g., Mason et al. 2005, Ricotta 2005, Petchey and Gaston 2006, Villéger et al. 2008). These indices usually describe two broad aspects of functional diversity: (1) how much of the functional niche space is filled by the existing species (functional richness) and (2) how this space is filled (functional evenness, functional divergence/variance).

Using functional diversity indices, however, entails several methodological problems. The first difficulty is the selection and the treatment of the traits, e.g., how many and which traits to use, how to weigh them, and how to combine them (Lepš et al. 2006, Petchey and Gaston 2006). Some solutions to these problems have been discussed and proposed by Lepš et al. (2006). The second set of problems is related to the indices themselves, i.e., do the indices measure exactly what the user wants to describe? Are the chosen indices independent from one another? Will diversity be measured for a single trait only or for a multivariate trait data set? Does the data set contain categorical and continuous variables? It is particularly important that these problems are considered carefully because ecological theories are developed and confirmed based on these results.

Some properties of selected indices were specified by Petchey and Gaston (2006) and Ricotta (2005), but new indices have been published since then (e.g., Cornwell et al. 2006, Podani and Schmera 2007, Villéger et al. 2008), and although the importance of intraspecific specialization and variability is clearly acknowledged (Bolnick et al. 2003), it has rarely been considered in the formalization of functional diversity. Moreover, a direct comparison of the different indices and their correlations with one another is still missing, and the user of functional diversity still faces the problems described here when selecting an index. The aims of this study were therefore: (1) to describe the main properties of the different functional diversity indices; (2) to propose new indices that enhance and supplement existing ones (e.g., accounting for intraspecific variability); (3) to test and compare the accuracy of all these indices in defined scenarios; (4) to measure the correlations among all these indices; (5) to summarize the results of 1–4 in a table to facilitate the selection of an appropriate index for the user.

METHODS

Functional diversity indices

The functional diversity of a community approached through the measurements of traits is usually described by three kinds of indices that can be combined to calculate different facets of functional diversity (Mason et al. 2005, Villéger et al. 2008; examples for application, Mason et al. 2007, 2008): functional richness (FR), functional evenness (FE), and functional divergence (FD). The FR indices generally measure how much niche space is filled, while FE and FD indices describe how this space is filled. Defining functional diversity indices, however, is not a simple task since there is no natural way of describing richness, evenness, or divergence when individuals are not assigned to classes (i.e., species), but rather described by their traits. First, any index should reflect the verbal definition of its properties. Second, FR, FE, and FD indices aim at measuring different aspects of functional diversity and should therefore be uncorrelated (independent) in a random community.

There are nine indices available in the literature to calculate functional diversity on the basis of measured traits, which we describe and test in this study: three FR indices (first described by Petchey and Gaston 2002, Mason et al. 2005, Cornwell et al. 2006), two FE indices (Mouillot et al. 2005, Villéger et al. 2008), and four FD indices (first described by Rao 1982, Mason et al. 2003, Lepš et al. 2006, Villéger et al. 2008). Each index group contains one- and multidimensional indices. Despite their multiplicity, these indices still miss some important points, e.g., FR indices do not consider individual variability. Indeed, individual variability in functional diversity has been approached through the expansion of existing indices for the use of individuals (Lepš et al. 2006, Cianciaruso et al. 2009). However, indices that specifically account for the use of intraspecific variation (using means and intraspecific variability as input, not individual trait values) have only been proposed for two FD indices (Lepš et al. 2006). To fill these gaps, we propose three additional indices (two FR indices and one FD index), which are also described and tested in this study.

Functional richness.—The FR indices measure how much of the niche space is occupied by the species present. They are usually interpreted by ecologists as an indicator for potentially used/unused niche space and thus, e.g., for productivity, buffering against environmental fluctuations, or vulnerability to invasion (Mason et al. 2005). Functional richness is naturally positively correlated with the number of species present (the more species there are, the larger the functional space occupied when species traits are somewhat randomly distributed). However, two communities with the same number of species may have different FR when functional traits of species are more closely clustered in one community than in the other. Functional richness is not weighted by species abundance.

1. *One-dimensional indices*.—Mason et al. (2005) suggested using the functional range (FR_R) as a measure of FR (Table 1: index number [IN] 1.1). Functional range is the relative range of a trait that is filled by a community at a site compared to the range of the trait for all communities together. In this way FR_R is restricted between 0 and 1 and becomes comparable for differently scaled traits. Please note, however, that the value for an individual site is not absolute but might change when the overall range changes (e.g., by the addition of a new site with species that differ in trait values). The community's range is calculated based on species' mean trait values by simply subtracting the lowest from the highest mean trait value at a site. The absolute range is calculated accordingly for all sites together. If more than one trait is used, the mean community range is then the mean of all traits.

Neither individual variability nor gaps in trait space are accounted for by FR_R. This is an issue when individual variability between sites differs and when functionally exceptional species are added to the community or when species with trait values within the range are missing. We therefore propose a new one-dimensional functional richness index (FR_{Is}) (Table 1: IN 1.2). The FR_{Is} is based on species' trait variability: instead of the community's trait range, FR_{Is} is based on the union of the species' trait ranges (and thus considers individual variability). It is calculated as the union of species' trait ranges at one site, relative to the union of species' trait ranges for all sites together (see FR_R). When calculating FR_{Is} the species' trait range can be calculated using two species/trait matrices as input tables, containing the species' minimum and maximum trait values, respectively. With this method, however, the range depends on the number of individuals measured. We therefore suggest using more conservative values, e.g., the 10th and 90th percentiles, confidence intervals, or the mean species trait value $\pm$ SD. For further details see Appendix A. A script in R for this index is *available online*.[2]

2. *Multidimensional indices*.—The multivariate counterpart of FR_R is the functional volume FR_V (Cornwell et al. 2006; Table 1: IN 1.3). The FR_V calculates the volume of trait space with the convex hull volume, which represents the smallest convex hull that encloses all species. With a complex algorithm, the most extreme points (vertices) can be determined and the volume encompassed by these vertices is calculated (TraitHull programmed in Python [Cornwell et al. 2006], *available online*;[3] and for R [Villéger et al. 2008], *available online*).[4] To calculate this index, the number of species must always exceed the number of traits.

A second existing multidimensional FR index is the dendrogram-based index FR_D (Petchey and Gaston 2002) (Table 1: IN 1.4). This index measures the extent of species complementarity based on a trait distance matrix (Petchey and Gaston 2002), a property equivalent to FR (Mouillot et al. 2005). A dendrogram is computed by hierarchical clustering; the functional richness is then the sum of the branch lengths of species present. There has been discussion in the literature on which distance measure and cluster method is best at calculating this index (Podani and Schmera 2006, 2007, Petchey and Gaston 2007, Mouchet et al. 2008). Here, we used the method developed by Mouchet et al. (2008; R program *available online*, see footnote 4) that computes dendrograms based on two distance matrices and seven clustering methods, which belong to the family of hierarchical agglomerative classifications and then selects the combination (including a consensus tree) that best represents the species distribution in functional trait space.

As for FR_R, FR_V does not consider gaps in functional trait space. We therefore developed a multivariate

[2] ⟨http://www.cemagref.fr/le-cemagref/lorganisation/les-centres/aix-en-provence/ur-hyax/scripts/ecology_schleuter2010/⟩

[3] ⟨http://www.pricklysoft.org/software/traithull.html⟩

[4] ⟨http://www.ecolag.univ-montp2.fr/software⟩

TABLE 1. Index number (IN), index abbreviation (IA), name, formula, and references for the different functional diversity indices.

IN	IA	Name	Formula	Source
1.1	FR_R	functional range	$\dfrac{\max_{s\in S_c}(X_{ts}) - \min_{s\in S_c}(X_{ts})}{\max_{s\in \cup S_c}(X_{ts}) - \min_{s\in \cup S_c}(X_{ts})}$	Mason et al. (2005)
1.2	FR_{Is}	functional richness (one-dimensional)	$\dfrac{\int \max_{s\in S_c}[\mathbf{1}_{st}(x)]\,dx}{\int \max_{s\in \cup S_c}[\mathbf{1}_{st}(x)]\,dx}$ where $\mathbf{1}_{st}(x)$ is 1 if x is between min and max, else it is 0 for categorical variables, L_{tc}/L_t	this study
1.3	FR_V	functional volume	the volume inside the minimum convex hull that encloses all species in functional space	Cornwell et al. (2006)
1.4	FR_D	functional dendrogram	distance matrices: Euclidean, Gower; clustering methods: single linkage, complete linkage, UPGMA, WPGMA, UPGMC, WPGMC, Ward's method	Petchey and Gaston (2002), modified by Mouchet et al. (2008)
1.5	FR_{Im}	functional richness (multidimensional)	$\int \max_{s\in S_c}\left(f_s(\mathbf{Z})\right)\,d\mathbf{Z}$ where $f_s(\mathbf{Z}) = \exp[-0.5(\mathbf{Z} - \mathbf{X}_s)^\top \boldsymbol{\Sigma}_s^{-1}(\mathbf{Z} - \mathbf{X}_s)]$	this study
2.1	FE_s	functional evenness (one-dimensional)	$\sum_{s=1}^{\lvert S_c\rvert-1} \min\left[\dfrac{\lvert X_{ts+1} - X_{ts}\rvert/(A_{ts+1} + A_{ts})}{\sum_{s'=1}^{\lvert S_c\rvert-1}\lvert X_{ts'+1} - X_{ts'}\rvert/(A_{ts'+1} + A_{ts'})}, \dfrac{1}{\lvert S_c\rvert - 1}\right]$ where species subscripts, s, are ranked by ascending order of trait value, t; for categorical variables: $\sum_{l=1}^{L_t} \min\left[\dfrac{A_l}{A}, \dfrac{1}{L_t}\right]$	Mouillot et al. (2005)
2.2	FE_m	functional evenness (multidimensional)	$\dfrac{\sum_{e\in E} \min\left[\dfrac{\mathrm{dist}(e)/(A_e/A)}{\sum_{e'\in E}\mathrm{dist}(e')/(A_{e'}/A)}, \dfrac{1}{\lvert S_c\rvert - 1}\right] - \dfrac{1}{\lvert S_c\rvert - 1}}{1 - \dfrac{1}{\lvert S_c\rvert - 1}}$	Villéger et al. (2008)
3.1	FD_{var}	functional logarithmic variance	$\dfrac{2}{\pi}\arctan\left[5\left(\dfrac{1}{T}\sum_{t=1}^{T}\sum_{s\in S_c}\dfrac{A_s}{A}\left(\ln X_{ts} - \overline{\ln X_{ts}}\right)^2\right)\right]$ where $\overline{\ln X_{ts}}$ is the mean of $\ln X_{ts}$ over all species present	Mason et al. (2003)
3.2	FD_σ	functional variance (FD_{var} modified)	$\sum_{s\in S_c}\dfrac{A_s}{A}\left(X_{ts} - \overline{X_{ts}}\right)^2$	Lepš et al. (2006)
3.3	FD_{cat}	functional unalikeability	$\mathrm{FD}_{cat} = 1 - \sum_{l=1}^{L_t}\left(\dfrac{A_l}{A}\right)^2$	Kader and Perry (2007)
3.4	FD_s	functional divergence (one-dimensional)	$\dfrac{Q_1(Y_t) - Q_3(Y_t)}{\max_{s\in S_c}(X_{ts}) - \min_{s\in S_c}(X_{ts})}$ where Y_t is a dummy variable that takes values X_{ts} with frequency A_s	this study
3.5	FD_Q	Rao's quadratic entropy	$\sum_{s\in S_c}\sum_{s'\in S_c}\dfrac{A_s A_{s'}}{A^2}\,\mathrm{dist}(s, s')$	Rao (1982), Champely and Chessel (2002)

TABLE 1. Continued.

IN	IA	Name	Formula	Source
3.6	FD_m	functional divergence (multidimensional)	$\frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + \overline{dG}}$ where $\Delta d = \sum_{s\in S_c} \frac{A_s}{A}(dG_s - \overline{dG})$, $\Delta\lvert d\rvert = \Sigma_{s\in S_c}(A_s/A)\lvert dG_s - \overline{dG}\rvert$, dG_s is the distance between species s and the gravity center of the convex hull (coordinates $G_t = (1/\lvert V\rvert)\Sigma_{s\in V}X_{ts}$) and $\overline{dG}$ is the mean value of dG_s over all present species	Villéger et al. (2008)

Notes: IN starting with 1, 2, or 3 and IA starting with FR, FE, or FD refer to functional richness, functional evenness, and functional divergence index groups, respectively. Subscripts s and m of index acronyms refer to single (one-dimensional) or multidimensional indices. Abbreviations: i, s, c, l, and t are individual, species, community, level of trait (for categorical variables), and trait subscripts, respectively; A_s, abundance of species s; A_{ts}, abundance of species s when species are sorted following trait t ascending ranking; A, total abundance of all individuals; A_l, abundance of trait level l; I_s, set of individuals of species s; L_{tc}, number of levels of categorical trait t covered by community c; L_t, total number of levels of trait t; L, total number of cross-trait levels; S_c, set of species present in community c ($\lvert S_c\rvert$, number of species present in community c); T, number of traits studied; V_c, set of vertex species from the convex hull in community c ($\lvert V_c\rvert$, the corresponding number of vertices); x_{tsi}, value of trait t in individual i from species s; X_{ts}, mean value of trait t in species s; $\mathbf{X}_s$, mean value of all traits in species s arranged in a vector; $\mathbf{Z}$, sample vector of all traits, used for the purpose of computing integrals over trait space; $\mathbf{\Sigma}$, variance/covariance matrix of traits; dist(s, s'), distance between species pairs based on mean trait values (for continuous variables, Euclidean distance is used; for discrete variables, the Gower distance is used); E, set of edges connecting species pairs in the minimum spanning tree; e, subscript of an edge; dist(e), distance between endpoint species of edge e; A_e, sum of the abundances of the endpoint species of edge e; Q_1, lower quartile; Q_3, upper quartile; UPGMA, unweighted pair group method using arithmetic averages; WPGMA, weighted pair group method using arithmetic averages; UPGMC, unweighted pair group centroid method; WPGMC, weighted pair group centroid method.

counterpart to FR_{Is}: FR_{Im} (Table 1: IN 1.5). The FR_{Im} index is specifically designed to account for individual variability and for gaps in the multidimensional functional trait space. The idea is to compute an equivalent "range union" (as for FR_{Is}) across species present in a community. To do so, each species s is assigned a function on trait space (f_s) that indicates whether a particular point in trait space is (or is not) occupied by species s (that is, whether species s trait values encompass this point). Here, we chose a simple form for f_s functions that uses information on both mean trait values and trait variance–covariance matrices for each species. FR_{Im} is then obtained as the integral of the maximum of all f_s functions (integrated over studied trait space). For further details see Appendix B. A script in Mathematica to calculate this index is *available online* (see footnote 2).

Functional evenness.—Functional evenness indices measure whether mean species traits are distributed regularly within the occupied trait space, i.e., with equal distances between nearest neighbors and equal abundances (a high FE index usually means a very regular distribution; a low FE index indicates the existence of separate clouds of species and/or abundances). Functional evenness indices are generally used to indicate under- or overutilization of resources and thus again productivity, reliability, and vulnerability to invasion (Mason et al. 2005). This index group includes species' abundances in its calculation.

1. *One-dimensional index.*—Based on Bulla's index for the measurement of species' evenness (Bulla 1994), the FE_s index (Mouillot et al. 2005) measures for each trait separately how evenly the trait values of all species present are distributed (Table 1: IN 2.1). First, the absolute, relative distances between the mean species trait values, in order of increasing values, is calculated and weighted by the sum of the relative species abundances. Second, if the distance is greater than $1/(S - 1)$ (with S representing species richness), it is replaced by $1/(S - 1)$, the distance, which is obtained for an optimal even distribution (Mouillot et al. 2005). FE_s is 1 if the distance between nearest neighbor species is exactly $1/(S - 1)$ and all species have the same abundances. The more a community differs from the optimal distribution in terms of abundance and trait difference, the lower the FE_s. When trait space is multidimensional, the community's evenness is the average of the FE_s calculated for each trait.

2. *Multidimensional index.*—The multivariate equivalent of FE_s is FE_m (Villéger et al. 2008; Table 1: IN 2.2). Instead of using the absolute distances between the species' trait values for each trait separately, this index uses the abundance-weighted distances between all species pairs to calculate first the minimum spanning tree (MST) that links all the species in a multidimensional trait space. The index then measures the regularity of the MST branch lengths, according to FE_s (i.e., comparison with the optimal branch length distribution).

Functional divergence.—The FD indices, finally, measure the variance of the species' functions and the position of their clusters in trait space (a high FD is caused by the clustering of species and/or abundances at the edges of the traits' space). The FD indices find application for indicating the degree of resource differentiation and thus competition (Mason et al. 2005), but they can also indicate a predominance of

extreme species. As FE, FD includes species' abundances in its calculation.

1. *One-dimensional divergence*.—Functional divergence can be calculated as the abundance-weighted functional variance using mean species values (Mason et al. 2003). Mason et al. (2003) suggested log transforming the trait values before calculating the variance (FD_{var}; Table 1: IN 3.1) and using species relative abundances as abundance weight. If more than one trait is used, FD_{var} is calculated for each trait separately and then averaged over traits. They recommend then using an arctangent transformation in order to restrict the index between 0 and 1. If species and/or abundances are clustered around the mean trait value, FD_{var} is low; if they are clustered at the edges of the community, FD_{var} is high.

The FD_{var} index is not applicable if the data set contains 0 values. To account for this problem, we propose using simply the abundance-weighted variance without log transformation (FD_{σ}; Table 1: IN 3.2) (Lepš et al. 2006). Since the variance is scale-dependent, traits should be standardized (e.g., centering and scaling by standard deviation) in case the trait space is multidimensional and the different traits have different scales. Another possibility is to use the coefficients of variation instead (i.e., standard deviations divided by means). Lepš et al. (2006) suggest including intraspecific variability in this index by adding the abundance-weighted intraspecific variance to the interspecific variance.

Since FD can also be understood as the relative range of the trait clustering, we propose a new one-dimensional index of functional divergence, FD_s. The FD_s index calculates the range of the zth percentiles (e.g., 25th percentile, Q_1, and 75th percentile, Q_3) relative to the overall range of each trait (Table 1: IN 3.4). The species abundance is accounted for by replicating the mean trait value of a species i times the species' abundance. This approach is conceptually different, since it is based on the relative span of the trait cluster and not on the variance. Low FD_s values indicate that half of the individuals in the community occupy a very confined functional space, independent of the position of that cluster along the trait axis; high values instead suggest that the functional space is more densely occupied at both its edges. For further details see Appendix C. A script in R to calculate this index is *available online* (see footnote 2).

2. *Multivariate divergence*.—The most common multivariate index of FD is Rao's quadratic entropy FD_Q (Rao 1982, Champely and Chessel 2002, Ricotta 2005; Table 1: IN 3.5). This index calculates the abundance-weighted variance of the dissimilarities between all species pairs. It is based on the Simpson diversity index (Simpson 1949) for the calculation of species diversity and weighs the trait-based distances between pairs of species [dist(s, s')] by the product of their relative abundances. Lepš et al. (2006) suggest calculating the species' pairwise dissimilarities through the sum of their overlaps for each trait. In this way, individual variability is included in this index and categorical and continuous variables can be mixed. Rao's quadratic entropy can also be calculated for single traits, the average of which leads to the same result as the multivariate approach, if the distance measure used is unchanged by averaging (e.g., Euclidean distance; Lepš et al. 2006). Since Walker et al.'s (1999) functional attribute diversity differs from Rao's quadratic entropy only in the way the distance matrix is calculated, it was not tested as a separate index in this study.

Villéger et al. (2008) proposed a new multivariate measure for functional divergence (FD_m). Based on the vertex species V of the convex hull (see FR_v), this index first determines the center of gravity G of the convex hull (Table 1: IN 3.6). It then computes the abundance-weighted deviances Δd of each species present from the species' mean distance to the center of gravity. In a last step, the index is restricted between 0 and 1. The FD_m index is low when species/abundances are close to the center of gravity and high when species and/or abundances are higher at the vertices of the convex hull. Since this index is based on the calculation of the convex hull, the same assumptions as for the calculation of FR_V must be met.

Transformation of trait data

Transformations of the original data should be avoided whenever possible. Nonetheless, one should always consider that some indices are not applicable to differently scaled traits (e.g., FD_{σ}). If at least one trait is scaled differently, all traits should be transformed; otherwise, this trait might have too little or too much weight in the index calculation. One possibility is to transform a trait that differs in several orders of magnitudes from the others using an algebraic function such as the logarithm (e.g., number of seeds in plants or number of eggs in fishes). Another possibility is to standardize the trait values with respect to the others, e.g., centering and scaling the trait by its standard deviation. This transformation has to be done for the overall data set and not on potential subsamples (e.g., at different study sites). The subsamples should then be drawn from the transformed trait matrix. For indices that calculate relative index values for each trait separately (e.g., FR_R, FR_{Is}, FD_s, etc.) and for one-dimensional indices, which range between 0 and 1 (e.g., FE_s, FD_{var}), the data need not to be transformed. Different transformation methods and their pros and cons are summarized in Lepš et al. (2006).

Accuracy of the indices

The first criterion for the quality of an index (accuracy) is the match between the way it actually behaves and the verbal definition of its properties (FR, FE, FD). This was tested in our study using an artificial data set (up to 25 species, two traits). We manipulated species composition and abundances in five tests (T1–

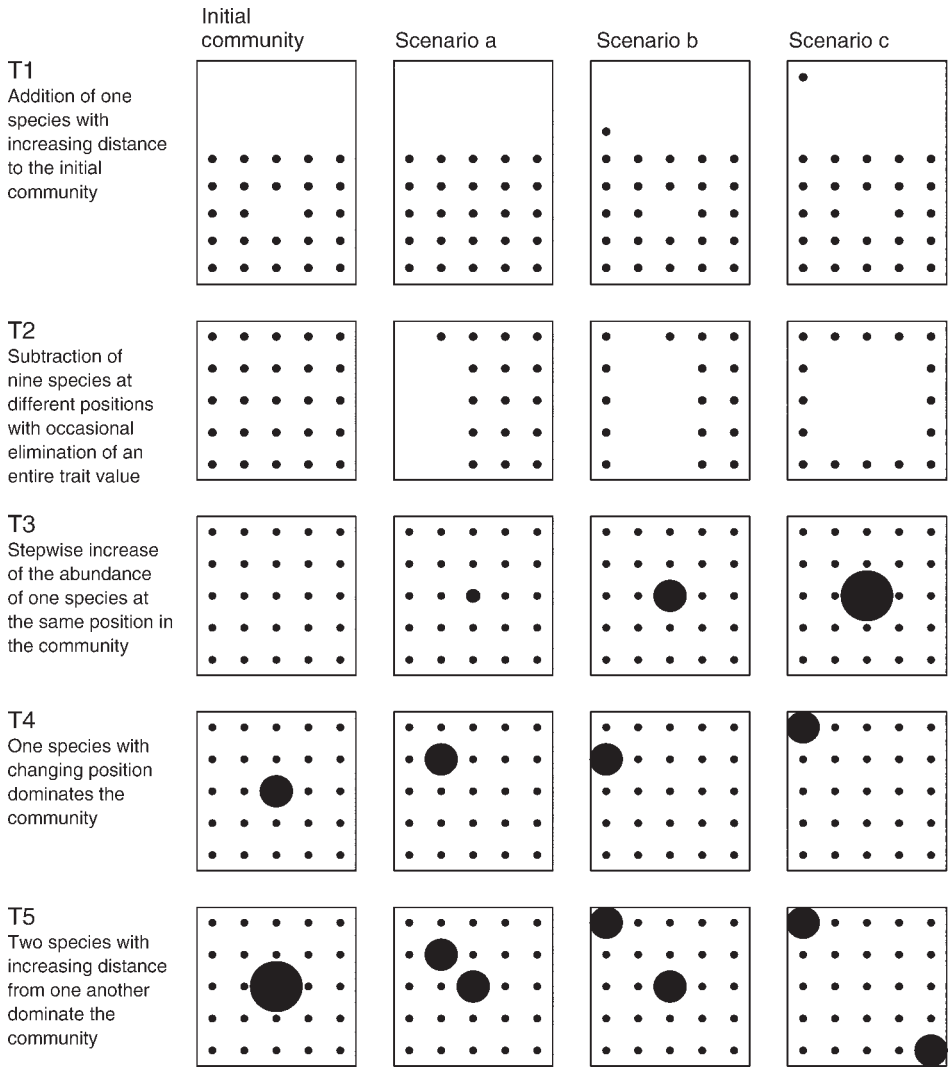
Initial community
Scenario a
Scenario b
Scenario c
T1
Addition of one species with increasing distance to the initial community
T2
Subtraction of nine species at different positions with occasional elimination of an entire trait value
T3
Stepwise increase of the abundance of one species at the same position in the community
T4
One species with changing position dominates the community
T5
Two species with increasing distance from one another dominate the community

FIG. 2. Illustration of the artificial scenarios used to test the behavior of the different indices. There are five different tests (T1–T5) whereby an initial community is modified three times in different ways (scenarios a–c). Each square represents one community with two trait axes; one dot within a square represents a species. The size of the dot indicates the abundance of the species (small dots reflect one individual, and with increasing size, 2, 25, and 250 individuals).

T5; Fig. 2) to compare the observed and expected changes of index values. Trait values were integer numbers between 1 and 5 for trait 1 and between 1 and 8 for trait 2. We assumed a standard deviation of 0.2 and a maximum deviation from the mean equal to 0.4 for all species and traits. In all tests, the initial species richness was 25, apart from T1, where it was 24. In T1 and T2 and, if not stated differently, in T3–T5, species abundance was set to 1 for all species.

The main aim of T1 and T2 was to test the effect of empty space in the trait space on the behavior of functional richness indices. In T1, we tested the effect of adding one species, with varying distance between the added species and the existing community (Fig. 2, T1). In T2, we removed nine species from the initial community. We removed these species so that either one trait value was eliminated completely, once at the outer edge of the community and once within the trait space (Fig. 2, T2 scenarios a and b), or the removed species were chosen in the middle of the trait space so that each trait value was present at least once (Fig. 2, T2 scenario c).

In T3–T5, the influence of varying species abundances on functional evenness and divergence was tested. In T3, we increased the abundance of one species stepwise from 1 (initial community) to 2, 25, and 250 individuals to test for the influence of the change in the abundance of one species (Fig. 2, T3). In T4, the influence of the position in trait space of a dominating species (25 individuals) was tested (Fig. 2, T4). In T5, we increased the distance between two dominating species (25 individuals each), starting from an initial community in which the

abundance of only one species was set to 50 individuals to simulate two identical species.

All indices were calculated for the initial community and for the different scenarios. The change in index values of the scenarios compared to the initial community was evaluated semi-quantitatively. We used the symbols "−," "+," and "=" to indicate whether the calculated value was higher, lower, or equal, respectively, compared to the initial community. The symbols were replicated to give a raw quantitative view of the changes (++, +++ with +<++<+++; −−, −−− with −−−<−−<−).

Indices correlation

The correlations among the different indices were tested using random communities. We computed 1000 randomizations for 14 different species richness levels (as multiples of five from five to 70) and three different numbers of traits (three, five, 10). The total number of treatments was 42 (14 × 3). Trait values were generated using uniform distributions between 0 and 1. The intraspecific standard deviation was considered to be 10% of the randomized trait value. Species abundances were randomized with a uniform distribution between 1 and 100 for each randomized trait matrix.

All indices described were calculated for each of the 42 000 random communities, apart from FR_{Im}, which was only calculated for the three-trait simulation. Actually, its computation time was very long on the computers used in this study, and it increased exponentially with the number of traits used.

To provide an overview of the relationships between different community indices, we used ordination techniques (e.g., PCA), which are known to perform well when summarizing complex data (Lebart et al. 2000). Since we had to compare a set of 42 matrices of 1000 rows (randomized communities) and 12 columns (indices), a single matrix-based approach was not appropriate. As a consequence, for each of the three trait levels, we used a multi-table ordination technique (e.g., Escofier and Pages 1994, Lavit et al. 1994, Chessel and Hanafi 1996) to assess the common structure of the 14 species richness-specific matrices. We performed a STATIS analysis (Lavit et al. 1994) to summarize the link between the different indices while removing the potential effect of species richness. This method is based on the optimization of the average ordination of the species richness-specific ordinations. The first step of STATIS consisted of calculating a matrix of scalar products between indices for each of the 14 levels of species richness. In a second step, the 14 rows × 14 columns matrix of the pairwise vectorial correlation coefficients (RV coefficients) between the scalar products' matrices was computed. The RV coefficient ranges from 0 to 1 and evaluates the extent to which two matrices share a common structure (Robert and Escoufier 1976). Then the matrix of RV values was diagonalized and the 14 coefficients of the first eigenvector were used to weight the 14 matrices of the scalar product between indices. A mean table of maximum inertia (called the reference structure) was subsequently computed as the weighted sum of the matrices of the scalar product between indices. By weighting the sum, greater importance was given to tables with similar structures, whereas lesser importance was given to the other tables. Finally, a PCA was performed on the reference structure. It provided the graphical representation of the common structure of the indices derived from the 14 species richness-specific tables.

Two groups of statistics synthesized the relevance and the efficiency of STATIS. The first statistics were the RV coefficients between two species richness-specific tables. The second statistical procedure used was the squared cosines ($\cos^2$) of the angles between the first axis scores of separate PCAs performed on each species richness-specific table and the first axis scores of the reference structure. This evaluates the match between the species richness-specific tables and the reference structure by using synthetic auxiliary variables.

Categorical variables

All the indices proposed so far (except those based on a distance matrix) cannot be computed for categorical variables. To address this problem, it is recommended in the literature to transform the data set from categorical to continuous variables via distance matrices and ordination methods, which allow a mix of continuous and categorical variables as inputs. Villéger et al. (2008) proposed calculating the Gower distance and then computing a principal coordinate analysis (PCoA). The trait values thus transformed (principal coordinate axis) can then be used to calculate the different functional diversity indices. Next to using the Gower distance with a PCoA, Hill and Smith's method can also be used (Hill and Smith 1976). This ordination technique combines discrete and continuous variables in a single analysis. If all variables are discrete, it is reduced to a simple correspondence analysis.

Although it is not really correct to transform categorical traits to continuous ones for the use of indices designed for real-valued variables, we consider these methods because they are commonly applied. Since continuous trait-based indices cannot be calculated for categorical traits it is impossible to assess the true effect of the transformation on the outputs (i.e., to compare the outputs for transformed and untransformed trait values). As a consequence, we only pseudo-tested the effects of these transformations using continuous traits as input. In this way, the normally calculated indices can serve as a reference value. As described above, we computed 1000 randomizations for six different species richness levels (in multiples of 10 from 10 to 60) with three traits. We then calculated all indices (1) with the original data set, (2) with the data set transformed via the Gower distance and PCoA (Podani

TABLE 2. Results for the five index tests, T1–T5 (as illustrated in Fig. 2): expected changes for the index categories (boldface) and observed changes of index values for the different scenarios compared to the initial community and in relation to one another.

	T1			T2			T3			T4			T5		
Index	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Richness	**+**	**+**	**+**	**−**	**−**	**−**	**=**	**=**	**=**	**=**	**=**	**=**	**=**	**=**	**=**
FR_R	=	+	++	−	=	=	=	=	=	=	=	=	=	=	=
FR_{Is}	=	+	+	−	−	=	=	=	=	=	=	=	=	=	=
FR_V	=	+	++	−	=	=	=	=	=	=	=	=	=	=	=
FR_D	++	+	−	−	−−	−−−	=	=	=	=	=	=	=	=	=
FR_{Im}	+	+	+	−	−	−	=	=	=	=	=	=	=	=	=
Evenness	**+**	**−**	**−−**	**−**	**−−−**	**−−**	**−**	**−−**	**−−−**	**=**	**+**	**++**	**−−−**	**−−**	**−**
FE_s	=	+	+	+	+	++	=	=	=	=	−	−−	=	−	−
FE_m	=	−	−−	−	−−	=	−	−−	−−−	=	=	+	−−	−	−
Divergence	**−**	**+**	**++**	**−**	**+**	**++**	**−**	**−−**	**−−−**	**+**	**++**	**+++**	**+**	**++**	**+++**
FD_{var}	−	+	++	−	+	++	−	−−	−−−	+	++	+++	+	++	+++
FD_σ	−	+	++	−	+	++	−	−−	−−−	+	++	+++	+	++	+++
FD_s	=	−	−−	+	++	+++	=	−	−	+	++	+++	+	++	+++
FD_Q	−	−−	−−−	−	+	++	−	−−	−−−	+	++	+++	+	++	+++
FD_m	−	−−	−−	−	+	++	−	−−	−−−	+	++	+++	+	++	+++

Notes: Symbols are: −, lower than initial community; +, higher than initial community; =, no change. The number of + and − signs indicates the increase compared to the other scenarios. See Table 1 for explanations of indices.

and Schmera 2006, Villéger et al. 2008), and (3) with the data set transformed using Hill and Smith's method (Hill and Smith 1976). The common structure of the three calculation methods was then assessed for each species richness level separately, using the RV values (i.e., the correlation coefficient between two tables) obtained from the method-specific tables.

All calculations and tests were carried out using the program R (R Development Core Team 2008). The STATIS analysis and the transformation via the Hill and Smith method and PCoA were computed using the ade4 package (Chessel et al. 2004, Dray et al. 2007).

RESULTS

Accuracy of the indices

Testing whether the indices behave according to the properties of the index group to which they have been assigned (FR, FE, FD) reveals that, among the FR indices, only two of them (FR_{Is} and FR_{Im}) accurately reflect the expected changes in functional richness (see Table 2: T1 and T2), because these indices consider empty space in the trait distribution of a community. However, FR_{Is} is only applicable to one-dimensional situations, while FR_{Im} well reflects functional richness in a multidimensional space. The results from scenario T1 c and scenarios T2 a and b show that when one trait value is missing in the entire data set, both indices decrease. However, in a multidimensional space, when none of the trait values of the removed species are unique, but their combination is, FR_{Im} is the only index that reflects these gaps properly (Fig. 2, Table 2: T1 scenario a, T2 scenario c). In contrast, indices such as functional range or volume (FR_R, FR_V) only reflect a decrease in functional richness when species are removed at the edge of the community. The dendrogram-based index for functional richness, FR_D, is furthest from the expected results for functional richness.

Among the two FE indices, the multivariate index FE_m behaves more adequately than its one-dimensional counterpart FE_s and matches the expected results quite well. Thus, FE_m can be considered an appropriate index (Table 2). However, this index fails to respond adequately in some cases, for example when species in the center of the community are added or subtracted (T1 scenario a and T2 scenario c). Species traits are then not evenly distributed over the entire functional space, but concentrated at the edges of the community, and thus the evenness is theoretically lower than in the initial community. Yet FE_m remains equal because the distribution of the branch lengths of the minimum spanning tree (the distance to the nearest neighbors) does not change. The one-dimensional index FE_s does not represent the distribution of species in a multidimensional trait space, but it reflects the evenness of the distribution for a single trait well (results not shown) and can be used if only one trait is considered.

All FD indices adequately match expectations. Even one-dimensional indices, averaged over all traits, accurately reflect changes in a multidimensional space (Table 2). Only in T1 do FD indices react differently: as expected, FD_σ and FD_{var} increase when a species outside of the initial community is added, whereas FD_Q, FD_m, and FD_s decrease.

Indices correlation

Species richness has a clear effect on the different indices, either in terms of variance or mean values (Fig. 3). Nevertheless, for all trait levels, there is a high similarity between the species richness-specific tables

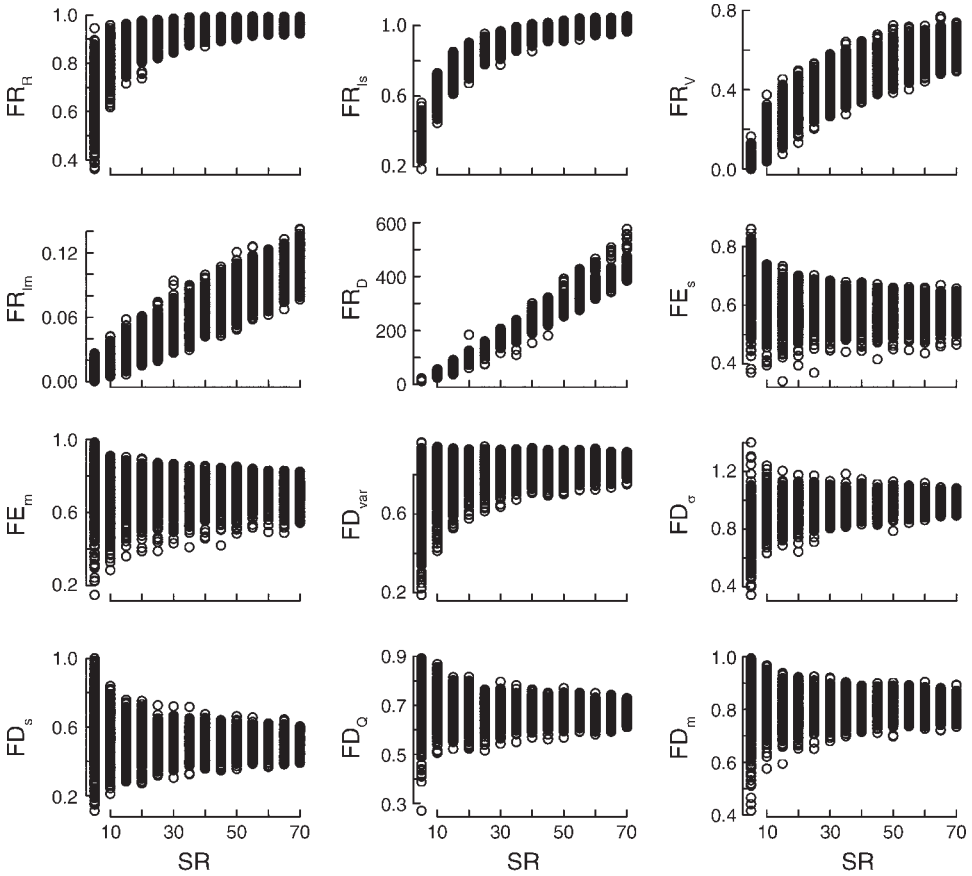

FIG. 3. Relationship of each of the 12 functional diversity indices with species richness (SR; 14 levels from 5 to 70), here for a data set with three different species traits. There are 1000 index values for each species richness level based on randomized trait and abundance data. Trait values and species abundances were generated using uniform distributions between 0 and 1 and between 1 and 100, respectively. See Table 1 for explanations of functional diversity indices.

(RV ranging from 0.885 to 0.996, from 0.945 to 0.998, and from 0.962 to 0.998 for three, five, and 10 traits, respectively). In addition, the $\cos^2$ confirms that the different reference structures reflect the structures of the individual species richness-specific tables ($\cos^2$ ranging from 0.905 to 0.944, from 0.920 to 0.940, and from 0.924 to 0.941 for three, five, and 10 traits, respectively). The lowest $\cos^2$ values are systematically found for the lowest levels of species richness (five, followed by 10) because of the higher variance of most indices at these species richness levels (see Fig. 3).

The reference structures over the different species richness levels are very similar for all trait levels (three, five, or 10; Fig. 4), confirming that there are several independent index groups that describe functional diversity. However, instead of the expected three axes corresponding to FR, FE, and FD indices, five axes are needed to explain the majority of the variance (74%) when FR_{Im} is included (three traits) and four axes without this index (77% and 78% for five and 10 traits, respectively).

The first axis is mainly correlated to the FD indices (FD_σ, FD_s, FD_Q, and FD_m; Table 3, Fig. 4). The fifth FD index (FD_{var}) is also correlated to the first axis, but with the second axis as well and it is overall more highly correlated to the FR indices FR_R and FR_V than to the other FD indices. Next to FD_{var} the second axis is correlated mainly to some of the FR indices (FR_R, FR_V, and partly FR_{Is}). The third axis represent functional evenness (FE_s and FE_m) and the remaining two FR indices (FR_{Im} and FR_D) are best represented by the fourth and fifth axes, respectively (Table 3, Fig. 4).

Note that FR_V is not fully independent of FD_Q and FD_s (r ranging from 0.09 to 0.59 for FD_s and from 0.21 to 0.71 for FD_Q depending on the species richness level and the number of traits), despite distance in the F1 × F2 factorial plane of the STATIS analysis. In addition, the correlation between FR_{Is} and FR_{Im} decreases with increasing species richness (from $r = 0.61$ in a community with five species to $r = 0.00$ in a community with 25 species).

Categorical variables

One- and multidimensional indices react differently to the transformation from discrete to continuous variables. Therefore, correlations between the method-

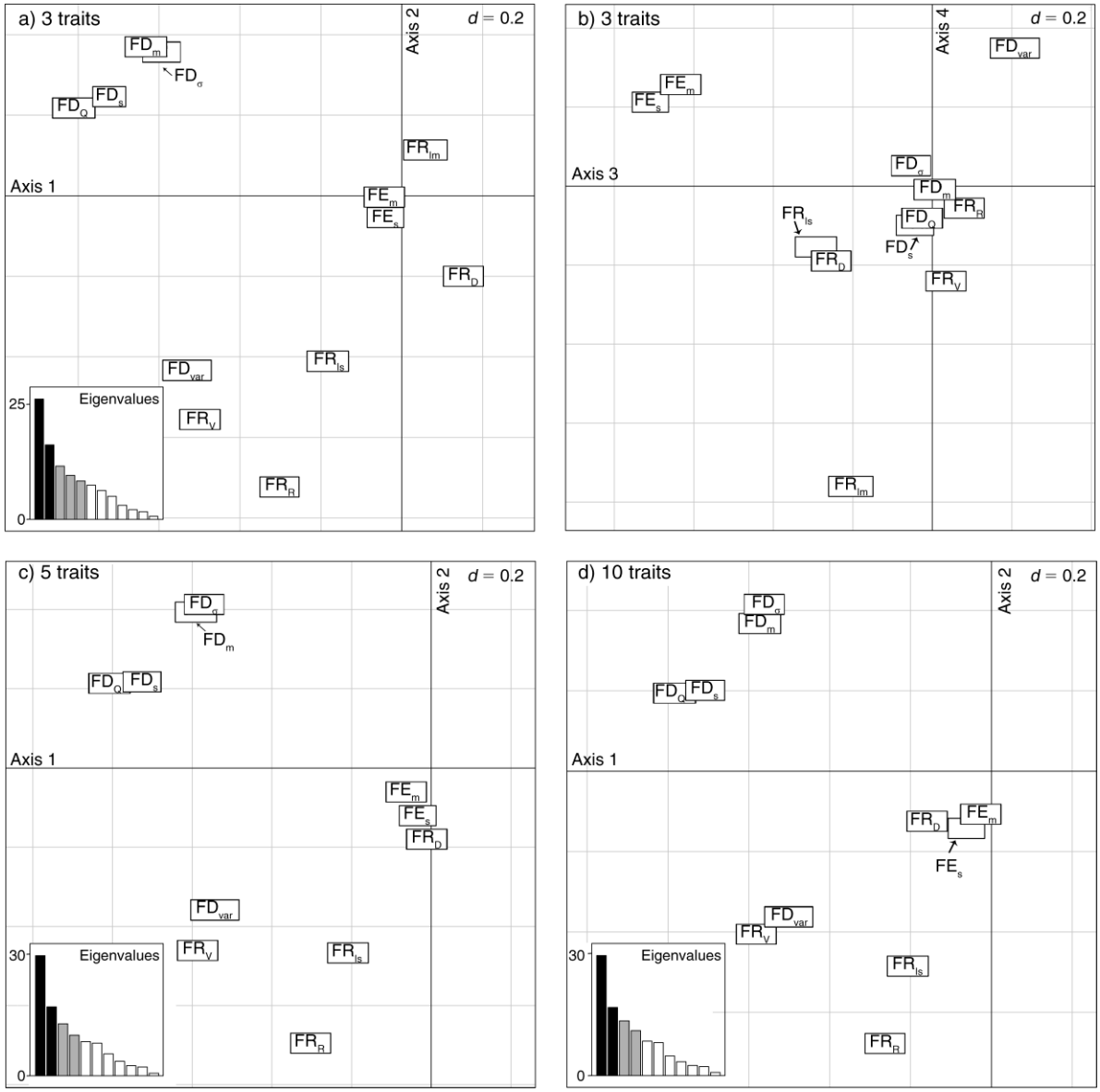

FIG. 4. Reference structures over the different species richness-specific ordinations gained from the STATIS analysis (Lavit et al. 1994). (a) Reference for three traits, first and second axes; axis 1 mainly correlates with FD indices, while axis 2 with FR indices. (b) Reference for three traits, third and fourth axes; the third axis mainly correlates with the two FE indices, axis 4 represents FR_{Im}. (c) Reference for five traits, first and second axes; axis 1 mainly correlates with FD indices, while axis 2 correlates mainly with FR indices. (d) Reference for 10 traits, first and second axes; axis 1 mainly correlates with FD indices, while axis 2 with FR indices. The insets display the eigenvalues (here expressed as percentage of contribution for the explanation of the variance, *y*-axis) of each axis (ordered from 1 to 12, *x*-axis). Shading of the bars refers to the importance of each axis, whereby white bars can be considered as statistical noise. The *d* values give the scaling of the grid. See Table 1 for explanations of functional diversity indices.

specific tables (RV values) have been computed separately for these two index groups. For multidimensional indices, we have found a high similarity between the index tables calculated with the raw data and the differently treated data sets. The transformation via the Hill and Smith method performs slightly better (RV range dependent on species richness between 0.897 and 0.956 for Gower distance and PCoA transformed data and between 0.997 and 0.999 for data transformed with the Hill and Smith method). That the results were worse for the transformation via the Gower distance and PCoA is mainly imputable to the calculation of FR_V (r with the index calculated with untransformed values ranged from 0.13 to 0.60, depending on species richness) and FD_Q ($r \sim 0.5$).

For the one-dimensional indices, neither of the transformation methods performs well (RV ranging between 0.605 and 0.894 for the transformation via

TABLE 3. Axis coordinates of the different functional diversity indices for the first five axes of the reference structure calculated with STATIS (Lavit et al. 1994) over the different species richness levels (here for a data set with three traits).

Index	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Richness					
FR_R	−0.30	**−0.72**	0.08	−0.06	0.09
FR_{Is}	−0.18	**−0.41**	−0.29	−0.15	**0.50**
FR_V	**−0.50**	**−0.56**	0.03	−0.24	−0.16
FR_D	0.15	−0.2	−0.26	−0.19	**−0.65**
FR_{Im}	0.05	0.11	−0.21	**−0.76**	−0.01
Evenness					
FE_s	−0.04	−0.05	**−0.71**	0.21	0.17
FE_m	−0.05	0.00	**−0.64**	0.26	−0.19
Divergence					
FD_{var}	**−0.54**	**−0.43**	0.20	0.35	−0.19
FD_σ	**−0.58**	0.36	−0.04	0.05	−0.13
FD_s	**−0.72**	0.24	−0.04	−0.10	0.05
FD_Q	**−0.80**	0.22	−0.04	−0.08	−0.04
FD_m	**−0.63**	0.37	0.01	−0.01	0.06

Note: Values lower than −0.4 or higher than 0.4 are boldface. For 1000 communities species richness trait values and species abundances were generated using uniform distributions between 0 and 1 and between 1 and 100, respectively. See Table 1 for explanations of indices.

Gower distance and PCoA and between 0.688 and 0.897 for transformation via the Hill and Smith method).

DISCUSSION

Performance of the indices

The functional diversity indices described and tested in this study performed quite differently. The quality of the indices aimed at describing the same aspect of functional diversity differed markedly, especially within the group of the FR indices.

In our view, the main criterion for the selection of an index is whether it accurately measures what it is intended to describe. This was the case for all FD indices, irrespective of whether they were one- or multidimensional, as well as for the two FE indices. However, while the multidimensional index FE_m performed quite well in describing the evenness in the two-dimensional space, its one-dimensional counterpart FE_s was only able to measure evenness when a single trait was considered. In contrast, the FR indices differed most strongly in their quality: the only indices that reflected the expected changes in FR, when species were removed within the functional trait space, were the two indices that consider gaps in the functional trait space (FR_{Is} and FR_{Im}). The FR_R and FR_V indices only partly reflected what is considered functional richness (only if there was a continuously filled trait space and species were removed or added at the edges of the community), while the results obtained from the index FR_D did not match the expected values. This index may work in some cases (Petchey and Gaston 2006), but it failed to pass the tests proposed here, perhaps due to the number of traits and/or the number of species used. The behavior of this index is thus difficult to understand, and we suggest rethinking its interpretation.

These results were confirmed by the multi-table ordination analysis (STATIS): instead of three principal component axes, which were expected to correspond to the three index groups FR, FE, and FD, we found that five axes were needed to explain most of the variance: three for FR and one for FD and FE. That three axes were needed to explain the variance of FR indicates that the existing FR indices describe independent aspects of functional diversity: FR_R and FR_V form one group, which describes the traits' range/volume; FR_{Im} measures the occupation and span of trait space; FR_D, which represents the branch length of a dendrogram, is independent of the other FR indices, but what it actually measures is difficult to determine. The FR_{Is} index was not represented by a single axis, but was partly correlated with FR_R, FR_V, and FR_{Im}, because FR_{Is} accounts for gaps in trait space (as FR_{Im}) but fails to take into account the multidimensional nature of trait space, so that gaps are severely underestimated when the number of traits is high.

The second criterion for the selection of an adequate index is that the chosen index is independent of indices describing other aspects of functional diversity. This criterion is met by the two FE indices, but not by all the FR and FD indices: FR_R and FR_V both correlated with FD_{var} and FR_V also correlated with FD_s and FD_Q (Table 4). This strongly suggests that FD_{var}, FR_R, and FR_V rather measure a mixture of functional richness and divergence.

Ricotta (2005) gave several other criteria for an index of functional diversity, which are only applicable to FR indices. For instance, an index should not decrease when a species is added (the monotonicity criterion) or should not increase when exactly the same species is added (the twinning criterion). These two criteria were also tested in

TABLE 4. Indices of functional diversity tested in this study, their properties, correlation with other indices, and their disadvantages.

Index	Source	Description	MD	*A* incl.	Use with cat. variables	Cor. with SR	Cor. with indices from other categories	Disadvantage	IN
Functional richness									
FR_R	Mason et al. (2005)	functional range	no	no	yes	yes	FD_{var}	no consideration of gaps, one-dimensional	1.1, 1.2 (cat.)
FR_{Is}	this study	individual's functional range	no	no	yes	yes	···	one-dimensional, intra-specific trait variation needed	1.2., 1.2 (cat.)
FR_V	Villéger et al. (2008)	functional volume	yes	no	no	yes	FD_{var}, FD_s, FD_Q	no consideration of gaps, SR has to exceed *N* traits	1.3
FR_D	Petchey and Gaston (2002)	sum of branch length of classification	yes	no	yes	yes	···	difficult to interpret, long computation time	1.4
FR_{Im}	this study	functional integral	yes	no	no	yes		long computation time, intra-specific trait variation needed	1.5
Functional evenness									
FE_s	Mouillot et al. (2005)	evenness of trait values	no	yes	yes	no	···	one-dimensional	2.1
FE_m	Villéger et al. (2008)	evenness of minimum spanning tree branch lengths	yes	yes	yes	no	···	···	2.2
Functional divergence									
FD_{var}	Mason et al. (2003)	logarithmic variance of traits	no	yes	yes	no	FR_R, FR_V	no 0 values possible	3.1, 3.3 (cat.)
FD_σ	Lepš et al. (2006)	variance of traits	no	yes	yes	no	···	···	3.2, 3.3 (cat.)
FD_s	this study	relative range of the distributional center	no	yes	no	no	FR_V	···	3.4
FD_Q	Rao (1982), Champely and Chessel (2002)	variance of distances between species	yes	yes	yes	no	FR_V	···	3.5
FD_m	Villéger et al. (2008)	mean deviation of the distance of the center of gravity	yes	yes	no	···	···	SR has to exceed *N* traits (see FR_V)	3.6

Notes: The table can be used to choose an index for the data set in question (dimensionality, type of variable, correlation with indices of a different category). Abbreviations are: *A*, abundance; Adapt., adaptation; cat., categorical; Cor., correlated; IN, index number; MD, multidimensional; *N*, number; SR, species richness. See Table 1 for explanations of indices.

the scenario test (Fig. 4, Table 2) and complied well with nearly all FR indices except FR_D.

In this study, we restricted our tests to classical versions of the indices without specific patterns of data distribution such as skewness. It would be of further interest to include hypotheses on the data randomizations and test how variations of a certain index (e.g., selection of the distance measure used in FD_Q) react under certain circumstances. However, we only expect slight fine-tuning and not fundamental deviations from the results presented here.

The use of categorical variables is problematic since most tested indices can only be applied to continuous variables. However, our pseudo-test with only continuous variables already revealed that the two transformations proposed (Gower distance followed by a PCoA and the Hill and Smith method) led to a loss of information. When tested for multivariate traits, this was especially true for the Gower distance transformation method followed by a PCoA; for one-dimensional indices, both index matrices calculated on the basis of transformed data correlated only weakly with the matrix based on the untransformed traits. This effect might be even worse when real discrete variables are included in the data set. In this case, the transformation methods via ordination techniques may not be the best choice for the treatment of categorical variables. One way to overcome this problem could be to use a multivariate index based

on a distance matrix (e.g., FD_Q) and to transform the trait matrix only via the Gower distance (Podani and Schmera 2006). Since the second transformation step (the ordination technique) is missing in this approach, we expect less loss of information. Another possibility is the approach suggested by Lepš et al. (2006), who recommend calculating dissimilarity between species pairs via the sum of their overlaps for each trait (continuous and categorical). In both approaches (Gower distance and summed overlaps), continuous and categorical variables share the same meaning and indicate just to which extent two species are identical.

Otherwise, discrete variables cannot be transformed to continuous variables and processed further with indices designed for this type of variable since functional evenness and divergence have no transposable meaning for discrete traits (i.e., no spatial evenness and divergence of discrete variables, but evenness or variability of trait-level distribution). Since categorical and real-valued variables are of completely different character, it is difficult to find an index in which they can be mixed up (for an exception see *Material and methods: Functional diversity indices: Functional divergence: Multivariate indices: FD_Q*). A second approach would therefore be to use indices aimed at measuring the specific properties of categorical variables. At present, we propose using the (one-dimensional) indices (as follows) designed to calculate species diversity, using trait levels instead of species.

The FR index (relative richness of trait levels).—Corresponding to the relative species richness at a site, we suggest using the number of trait levels present at a site as a proportion of the number of trait levels for all communities together (see FR_{Is}; Table 1: IN 1.2).

The FE index (evenness of trait-level distribution).—We suggest using Bulla's index of species' evenness (Bulla 1994) based on the contribution of a trait level (A_l) to the overall sample size A (total number of individuals) (see FE_s; Table 1: IN 2.1).

The FD index (variability of trait-level distribution).—We suggest using the "index of unalikeability" FD_{cat} by Kader and Perry (2007; Table 1: IN 3.3), which corresponds actually to the Simpson index of species diversity (Simpson 1949) but uses trait levels instead of species. The FD_{cat} represents the proportion of possible comparisons, which are unalike, by calculating the contribution of a factor level (A_l) to the overall sample size A and subtracts the sum of the squares from 1.

Note that for categorical variables, FE and FD measure approximately the same thing, since both reflect the equitability of distribution (Smith and Wilson 1996). The proposed and other indices on species diversity have been extensively tested (e.g., Washington 1984, Smith and Wilson 1996, Beisel et al. 2003).

Recommendations for users

Based on the criteria discussed above and the tests performed, we recommend using the multidimensional index FR_{Im} to measure FR or FR_{Is} if only a single trait is considered. Both indices account for intraspecific variability and consider the existence of empty space within the functional trait space and therefore reflect the true functional richness of the community better. Besides, these indices are orthogonal to FE and FD indices. If the user decides to compute FR through FR_V, the data set should not be transformed, even in the case of differently scaled traits, since the convex hull calculated with transformed data does not properly represent the functional richness for geometrical reasons, but correlates negatively with the expected results and the other indices for functional richness (results not shown).

The FR indices are naturally correlated to species richness. When indices of different communities are compared with one another or when differences between communities are explained with predictor variables, the effect of species richness should therefore be removed from the observed pattern, in order to describe patterns of pure functional diversity. Since the observed relationships are not simply linear and differ between the FR indices and because of unequal variances, we recommend using null models to remove the effect of species richness rather than using the residuals from a constructed model (method, Gotelli and Graves 1996; example for application, Mason et al. 2007, Prinzing et al. 2008).

Both FE_s and FE_m can be used to calculate FE. The use of FE_s is, however, narrowly restricted to one-dimensional data sets. Similarly, we cannot recommend the use of a specific FD index because all indices reflect the expected changes well, irrespective of whether they are one- or multidimensional. However, it should be remembered that not all FD indices are independent of FR indices (Table 4), seemingly because FD_{var} and some FR indices measure a mixture of FR and FD properties. Further, it should be mentioned that indices based on a distance matrix allow for the use of categorical and continuous variables simultaneously, and they can include intraspecific variability when calculated via the pairwise trait overlap as suggested by Lepš et al. (2006). Specific disadvantages of all indices are further summarized in Table 4.

Concerning categorical variables, we recommend at present avoiding their use, if possible, or using indices based on a distance matrix or the one-dimensional indices of species diversity (Table 1: IN 1.2, 2.1, 3.3). In this case, however, the user should keep in mind that the indices designed for categorical variables (especially for FE and FD) do not have the same meaning as their continuous counterparts. The results for the different traits should therefore be averaged over continuous and categorical variables separately, rather than directly averaged over all traits.

In real world measurements, the user comes to face more problems apart from choosing the right index,

many of which (e.g., weighing of traits) are discussed in Lepš et al. (2006) and Petchey and Gaston (2006). One frequently occurring problem is that normally not all trait values can be measured for each individual. This is, however, not a problem for the calculation of the indices, since the calculation of all indices (including the newly proposed indices that include intraspecific variability) is based on mean trait values and their variability. And how many individuals should be measured for each species? In general the more, the better. However, to restrict sampling effort, a reference value could be the amount of individuals that are necessary to describe the species' trait distribution (Cianciaruso et al. 2009).

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APPENDIX A

One-dimensional functional richness (FR_{Is}) (*Ecological Archives* M080-016-A1).

APPENDIX B

Multidimensional functional richness (FR_{Im}) (*Ecological Archives* M080-016-A2).

APPENDIX C

One-dimensional functional divergence (FD_s) (*Ecological Archives* M080-016-A3).